



Siphonaria funiculata REEVE (SIPHONARIIDAE, PULMONATA): A REDESCRIPTION MAKING *S. virgulata* HEDLEY A GEOGRAPHICAL VARIANT OF *S. funiculata*.

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SUMMARY

Based upon the examination of anatomical features and shell morphology *Siphonaria funiculata* Reeve, 1856 and *S. virgulata* Hedley, 1915 from southeastern Australia are considered to be synonymous, the former having systematic priority. Characters previously considered of specific value, particularly shell and radular, are shown to be widely variable. Investigation of geographical shell variation indicates that the nominal species *S. virgulata* is a clinal variant of *S. funiculata* at the northern end of its geographical range.

INTRODUCTION

The patelliform shell of the Siphonariidae shows wide specific and geographical variation (Hanley, 1858; Angas, 1867; Hubendick, 1950, 1954; Marcus and Marcus, 1960). The non recognition of such variability coupled with incomplete descriptions (i.e. no anatomical features), based upon features of worn shells or insufficient material, has resulted in a confused literature confounded with misidentifications and misinterpretations of existing descriptions.

As part of a revision of Australian Siphonariidae, redescrptions of *S. funiculata* and the nominal species *S. virgulata* are presented and their synonymy proposed, based upon examination of type specimens and anatomical features.

Characteristic forms of these synonyms are designated in this paper as geographical variants of *S. funiculata* (which has systematic priority), and subsequently referred to as the typical *S. funiculata* and the nominal *S. virgulata* forms to distinguish them from the redescrbed specific form.

S. funiculata belongs to the subgenus *Liriola* Dall, 1870 and "section Pachysiphonaria" Hubendick, 1945.

MATERIALS AND METHODS

All of the material examined, except where noted, is in the collections of The Australian Museum (A.M.)

The buccal mass, reproductive system and spermatophore were dissected from several specimens preserved in 5% neutralized formalin. The radula was removed by macerating the buccal mass in concentrated KOH for 24 hours. After being thoroughly washed with distilled water the ribbon was stored in 70% alcohol. Radulae and spermatophores were

either slide mounted and examined and counted through a compound microscope or affixed to a microscope-slide slip fragment, mounted on a stub, coated with gold and examined under a scanning electron microscope (SEM). In most sample lots the anatomy and shell of several specimens were examined to determine variation. The radial shell ribs on a line 1 cm in diameter from the shell apex were measured and counted. Measurements of shell length, width and height using a caliper, were recorded from 30 specimens of the typical *S. funiculata* and the nominal *S. virgulata* forms throughout their respective distributions. In all similar rib counts and shell measurements were recorded for each of 15 shells of mixed populations from six geographical regions (i.e. N.NSW., Syd. NSW., E. Vic., Westernport Vic., W.Vic and Tas.). The means, ranges and standard deviations were calculated for these rib counts, single shape dimensions (i.e. length, width, height and rib width) and quotient ratios of length:width, length:height, width:height and length:width:height. Single shape dimensions and ratios were used as measures of specific and geographical shell variation. The use of ratios in comparisons reduced the bias of sample age and/or locality exposure variation existing within single shape variables. The specific data were subjected to a single classification two tailed analysis of variance for the parametric single shape variables and a Wilcoxon Test for the non-parametric ratio variables (Sokal and Rohlf, 1969, p. 400). Geographical data were subjected to a Kruskal-Wallis test of variance (Sokal and Rohlf, 1969, p. 388) and where significant geographical variation existed a multiple comparison test of the means (Sokal and Rohlf, 1969, p. 396) indicated an ordered relationship between geographical populations. Critical values are from tables in Rohlf and Sokal (1969).

TAXONOMY

Siphonaria funiculata Reeve, 1856

TYPES: Holotype, British Museum (Natural History) (B.M.N.H.)

M.C. 197927. Paratypes (3) B.M.N.H. M.C. 197927

TYPE REFERENCE: Conchologia Iconica IX *Siphonaria*, pl. 2, fig. 6

TYPE LOCALITY: Tasmania.

DIMENSIONS	length mm	width mm	height mm
Holotype	24.3	17.9	13.9 (pl. 1b,c).
Paratypes	25.7	20.2	11.3
	21.9	16.5	8.9
	19.7	15.7	7.2
figured specimen from Reeve's description	26.1	18.2	—
large specimen A.M. Coll.	33.9	24.3	15.9
small specimen A.M. Coll	2.5	1.7	0.9

REMARKS

Hubendick (1946) includes several incorrect bibliographic synonyms for *S. funiculata*; *S. lirata* Reeve, 1856, is not a "clerical error" but a synonymous species described without locality data, by Reeve, 1856, mislabelled as *S. funiculata* and corrected in an errata note in the same volume (overlooked by most authors); *S. laeviuscula* (= *funiculata* in Hutton, 1878) which, as stated by Hutton (1878), has doubtful locality data, (*S. laeviuscula* Sowerby, 1835 is a South American species absent from the western Pacific, in particular New Zealand where Hutton's material is claimed to have been collected); *S. zonata* T. Woods, 1879b, in Tate and May (1901, not 1902 as in Hubendick, 1946) is a misidentification and compared with T. Woods' (1879b) description, a synonym of *S. tasmanica* T. Woods, 1876.

T. Woods (1879a) states that *S. funiculata* is a pale variety of *S. diemanensis* (sic) Quoy and Gaimard, 1833 (= *S. diemenensis*) suggesting both are variants of *S. denticulata* Quoy and Gaimard, 1833)

= *Siphonaria blainvillei* Hanley, 1858

TYPE: Holotype B.M.N.H. 1907. 10.28.90 (pl. 1a).

TYPE REFERENCE: Proc. Zool. Soc. Lond. 26: 151-153.

TYPE LOCALITY: Unknown.

DIMENSIONS	length mm	width mm	height mm
Holotype	22.6	18.1	13.2

REMARKS

The description of this nominal species was based upon a single worn shell specimen. Examination of the holotype indicates it is a tall, broadly ribbed specimen of *S. funiculata* (also observed by Hedley (1915)). This nominal species was synonymized with *S. funiculata* by Hubendick (1946).

= *Siphonaria virgulata* Hedley, 1915

TYPES: Holotype A.M. C.39858, Paratypes (20) A.M. C.39858

TYPE REFERENCE: Proc. Linn. Soc. NSW. 39: (4) 751, pl. 85, figs 96-8.

TYPE LOCALITY: Terrigal, near Gosford; Sydney: Twofold Bay, NSW. C. Hedley Coll. (labels with types only record Terrigal, NSW; original description states 3 type localities).

DIMENSIONS:	length mm	width mm	height mm
Holotype	12.9	10.4	3.9
Paratypes (20)			
\bar{x}	10.5 (sd = 2.5)	8.3 (sd = 2.2)	3.6 (sd = 1.0)
large paratype	16.5	14.3	6.2
small paratype	7.7	5.8	2.6
measurements from Hedley's description	21.0	19.0	9.0
large specimen A.M. Coll	23.0	18.9	11.7
small specimen A.M. Coll	2.3	1.1	0.3

DESCRIPTION

Distribution and habitat.

S. funiculata is confined to eastern Australia ranging from Tas. (latitude 43°40'S) and Apollo Bay, western Vic. (38°46'S, 143°40'E) (not west of Cape Otway, Vic. (Bennett and Pope, 1953)) to Burnett Heads, near Bundaberg, Qld. (24°45'S, 152°25'E) (fig. 1).

Relative to the biogeographical provinces described by Bennett and Pope (1953) this species is termed cool temperate (Maugean) to tropical (Solanderian). *S. funiculata* commonly occurs on exposed rocky shores in the mid and upper littoral zones often on dry bare rock (Creese, 1980). Associated zone forming indicator organisms include the barnacles *Catophragmus polymerus* Darw. (NSW.-Tas.) and *Tesseropora rosea* (Krauss) (Qld.-NSW.), and the mussel *Brachyodontes rostratus* (Dunk.) (NSW.-Tas.) in the upper littoral zone and the serpulid worm *Galeolaria caespitosa* (Savigny) (Qld.-Tas.) in the mid littoral zone.

The two shell forms characterized by the typical *S. funiculata* and the nominal *S. virgulata* forms, have southern and northern distributions respectively, merging to a transition shell form (described in geographical variation below) between Mallacoota (37°35'S, 159°45'E,) and Lakes Entrance (37°45'S, 147°58'E), eastern Vic. The isolated occurrence of the northern *virgulata* shell form in Western Port, Vic. is attributed to southwardly dispersed larvae penetrating cool currents and finding the shallow, warm bay water, a physiologically suitable environment for adult development. Both Hedley (1915) and Iredale (1924) suggest this form is the northern biogeographical equivalent of the southern shell form, the typical *S. funiculata*.

External features of the animal (preserved specimens).

The foot side tissue and visceral mass are grey to brown with a pale to cream foot sole. The dark, smooth tissue of the side of the foot has white internal (subepithelial) spots,



Figure 1. The distribution of *S. funiculata* and dispersal of population samples (hatched areas) used to determine nature of geographical shell variation.

corresponding to unicellular mucous glands, described by Marcus and Marcus (1960), fairly evenly distributed around the foot, but becoming more vivid and dense close to the foot sole. The head is inconspicuous. Two small, black, epithelial "eye" spots are centralized on two, thick centrally touching cephalic folds, that extend anteriorly in front of the mouth. These folds have numerous, clustered, white mucous cells similar to those of the foot side tissue, but smaller. Between the mantle and the side of the foot, covering the pneumostome, is a pale anal lobe, extending to the shell lip between the anterior and posterior adductor muscles. The mantle (often folded in preserved specimens) is loose, covering the adductor muscle. It is coloured with a cream to white fringing band and inner alternating brown and white patches (corresponding to mantle pigment cells) aligned with the shell lip colouration. The genital pore is indistinct. The animal's external features have not been previously described. Mucous glands and pigment cells are similar in size and dispersal to other Australian *Siphonaria*. Several animals collected from Warden Head, Ulladulla, NSW, are a tissue colour variation, being uniformly red brown, matching their internal shell colour.

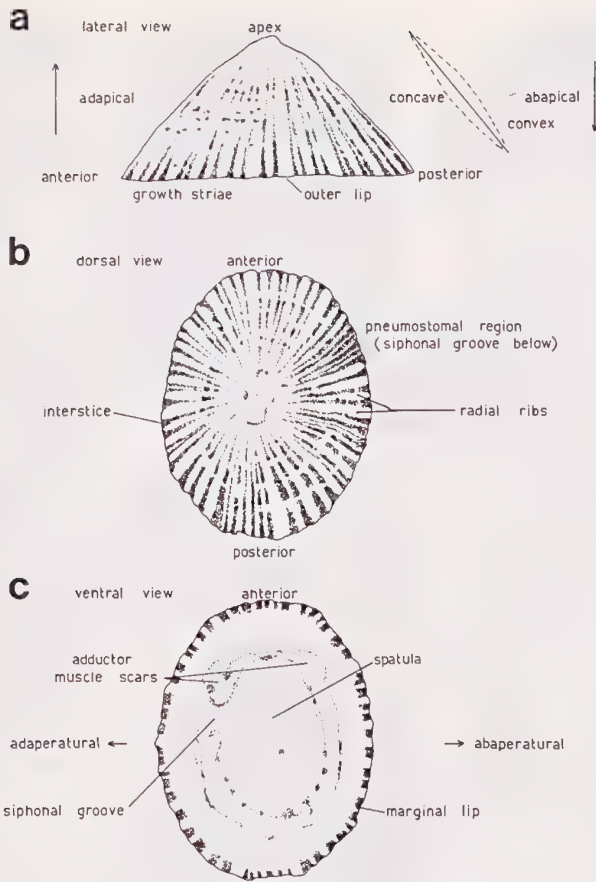


Figure 2. Schematic representation of shell morphology terminology.

Shell (figs 2a, b, c; pls. 1b-1, 2a-k).

The shell morphology of *S. funiculata* is widely variable, a feature common to other *Siphonaria* species (Reeve, 1856; Hanley, 1858; Angas, 1867; T. Woods, 1879a; Hubendick, 1946, 1950, 1954).

The shell is patelliform, thin, ovate and assymetrical with a subcentral apex offset posteriorly and adaperaturally (fig. 2b). Exterior sculpture is finely costate with irregularly spaced radial ribs and growth striae both of which are adapically discontinuous. The ribbing is flat and broad with rib widths ranging from 0.39 to 1.89mm (sd =, \bar{x} = 0.82, n = 30). The white axial ribs, often bistrate with chocolate interstices, narrow and curve adapically. The number of ribs ranges from 28 to 94 (sd = 10.5, \bar{x} = 63, n = 60). The apical sides are weakly convex (fig 2a). The apex is often eroded creating a white spot. The siphonal groove is weakly visible with fine, clustered, brown radial striae above a slight fold in the marginal lip. The interior is polished and purplish brown with a white to blue spatula (colouration extends into the shallow siphonal groove) fading to a chocolate brown zone above the brown adductor muscle impression and tan margin. The marginal lip is shallowly scalloped with alternating chocolate brown and white radial markings, restricted to the lip margin and reflecting the exterior ribbing. The adductor muscle impression is "C" shaped with a thin, lightly convex, anterior attachment area and a bare siphonal groove flanked by broad, ovate muscle impressions (fig. 2c). Juvenile specimens have fine radial ribs, a dark

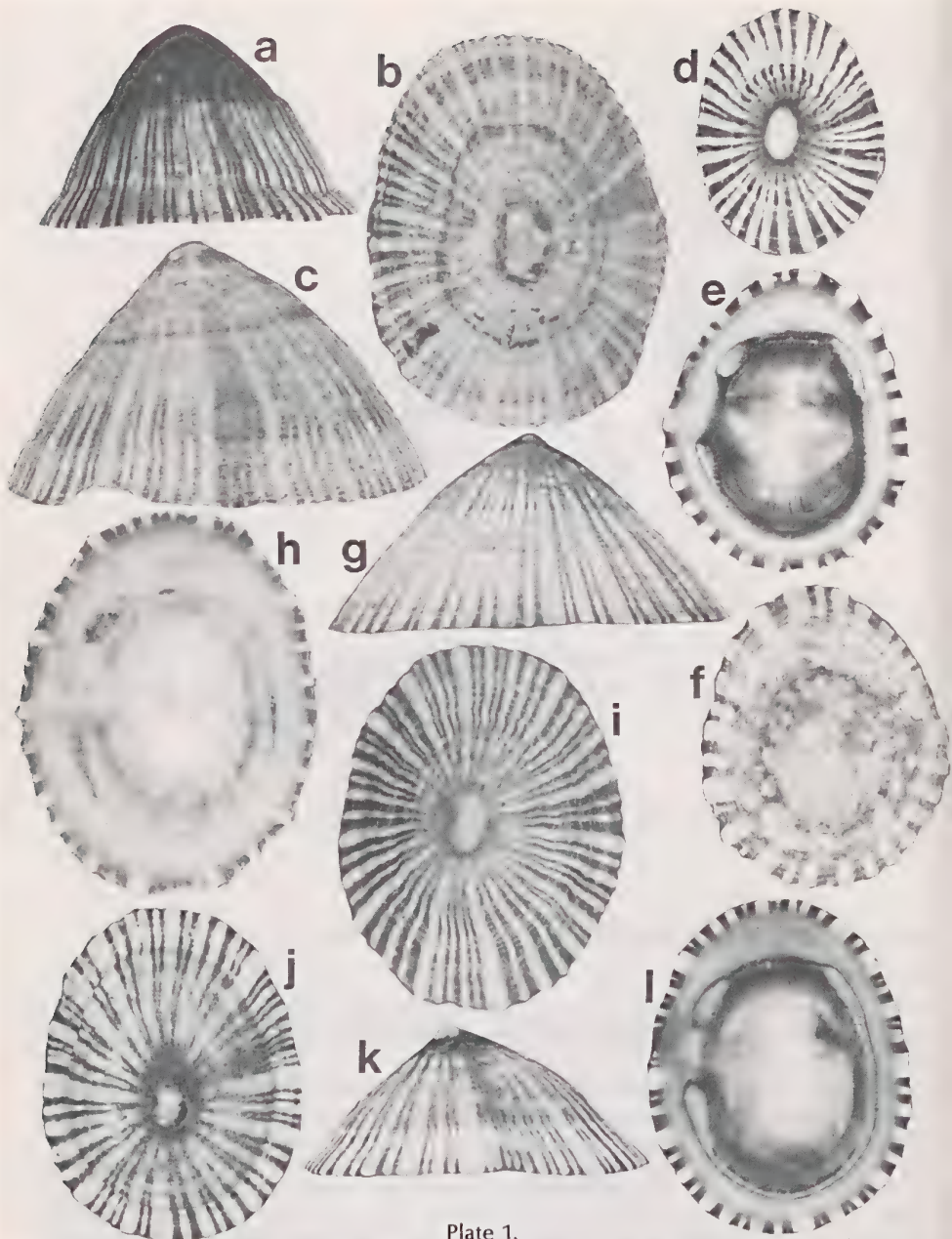


Plate 1.

S. funiculata; the anterior of dorsal and ventral views is aligned with the top of the page; a. nominal species. *S. blainvillei*, holotype. adaperatural lateral view $l=22.6\text{mm}$, $h=13.2\text{mm}$; b. and c. *S. funiculata*, holotype, adaperatural lateral and dorsal views, $l=24.3\text{mm}$, $h=13.9\text{mm}$; d. typical *S. funiculata* form, Ocean Beach, Vic., dorsal views, $l=20\text{mm}$; e. and f. Apollo Bay, Vic., ventral and dorsal views, $l=19\text{mm}$; g. Port Sorell, Tas., abaperatural lateral views, $l=23\text{mm}$, $h=12.7\text{mm}$; h. and i. Port Arthur, Tas., dorsal and ventral views, $l=22\text{mm}$, $w=17\text{mm}$; j. and k. Ocean Beach, Vic., dorsal and adaperatural lateral views, $l=20\text{mm}$, $h=9\text{mm}$; l. Lorne, Vic., ventral views, $l=20\text{mm}$, $w=16\text{mm}$.

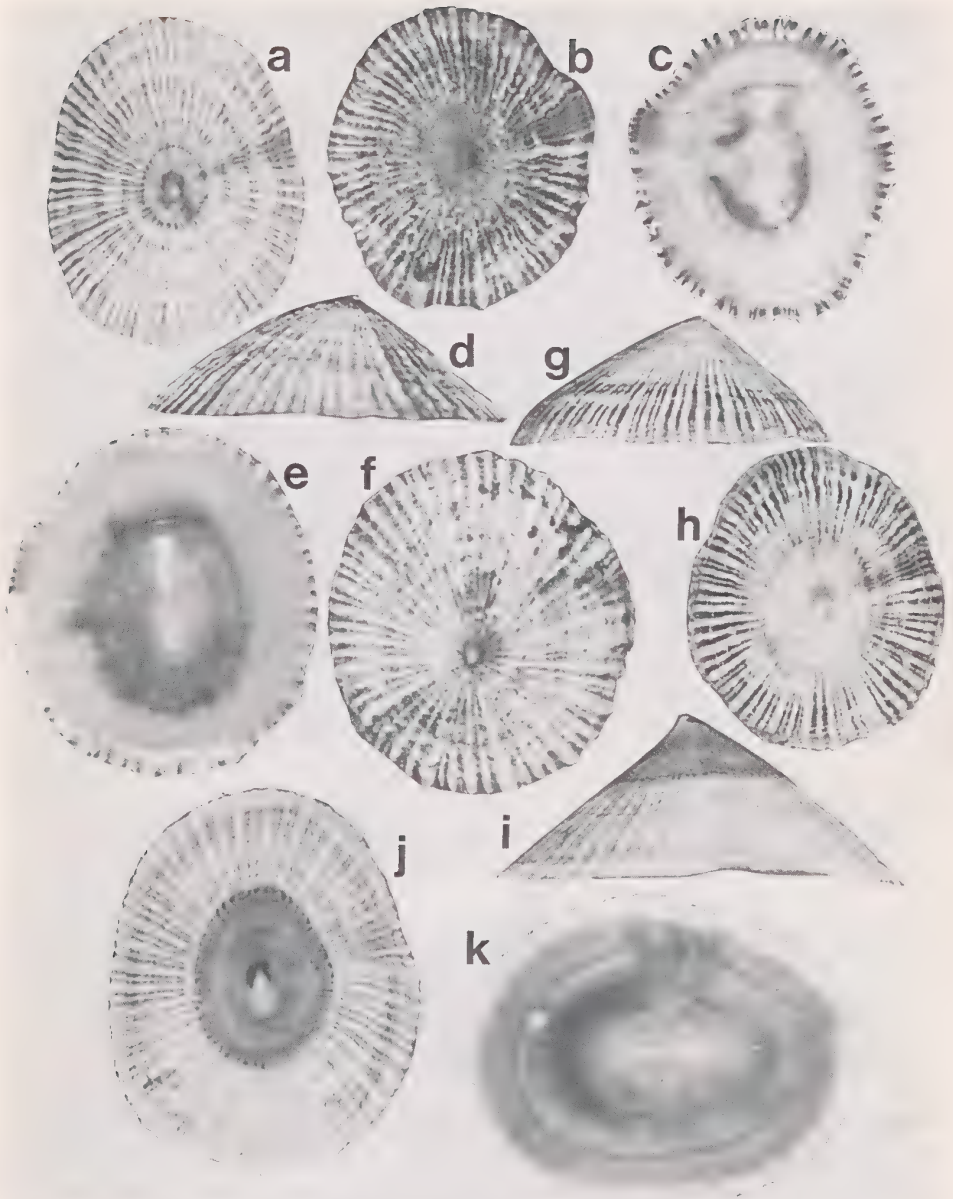


Plate 2.

S. funiculata. Nominal species *S. virgulata* form; except for lateral views and k, shell anterior is aligned with the top of the page; a. McMasters Beach, NSW., dorsal view, l=19mm; b. and c. The Caves Beach, S. of Swansea, NSW., dorsal and ventral views, characteristic *virgulata* form, l=18mm; d., e. and f. Lakes Entrance, Vic., abaperatural lateral, ventral and dorsal views, l=21mm, h=7mm; g. and h., Point Lookout, Stradbroke Is., Qld., abaperatural lateral and dorsal views, l=18mm, h=7mm; i., j. and k. Western Port, Vic., abaperatural lateral, dorsal and ventral views, l=24mm, h=10mm.

brown interior and exterior (often obvious around the apex of adult specimens), with a white spatula.

Reproductive system.

This system in *Siphonaria* is a complex hermaphroditic system. Apart from slight variations between individuals, the size, shape and colour of reproductive organs are the same (fig. 3a).

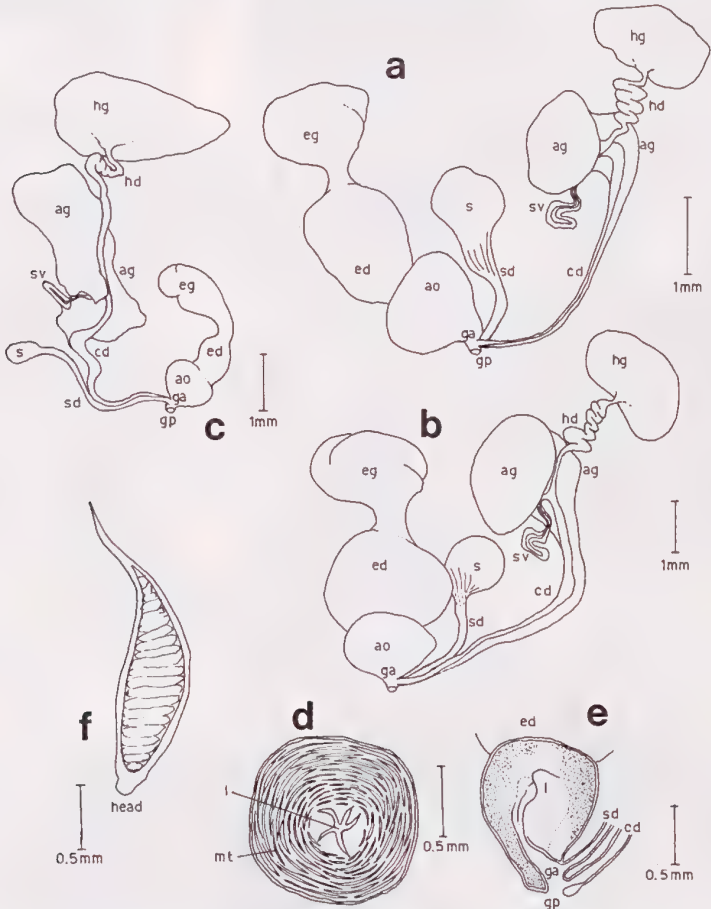


Figure 3. Reproductive organs and spermatophore of *S. funiculata* and *S. tasmanica*.
 a. Typical *S. funiculata* form, Red Bluff, Lakes Entrance, Vic. lengths — shell 14mm, animal (preserved) 10mm.
 b. Nominal species *S. virgulata*, Warden Head, Ulladulla, NSW. lengths — shell 22mm, animal (preserved) 16mm.
 c. *S. tasmanica*, Port Campbell, Vic: lengths — shell 10mm, animal (preserved) 7mm.
 d. Longitudinal section of accessory organ.
 e. Transverse section of accessory organ.
 f. Spermatophore.

ag — albumen gland, ao — accessory organ, cd — common duct, ed — epiphallus duct, eg — epiphallus gland, ga — genital atrium, gp — genital pore, hd — hermaphrodite duct, hg — hermaphrodite gland, l — lumen, mt — muscle tissue (connective), s — spermatheca, sd — spermathecal duct, sv — seminal vesicle.

The tough white epiphallus gland and duct and accessory organ fill the region between the anterior adductor muscle and the buccal mass. Both the epiphallus gland and duct are smoothly ovate possessing thick fibrous layers of muscle tissue enclosing a penial complex. The duct is larger than the gland and often elongated. Figures 3c, d show cross sections of the accessory organ with a folded lumen. No flagellum occurs on the epiphallus gland. The genital atrium opens directly from a protuberance on the accessory organ to an exterior adaperatural pore below the mantle on the side of the foot, anterior to the pneumostome. The hermaphrodite gland (ovotestis) is situated below the mantle cavity in a posterior adaperatural position over the foot muscle tissue. This gland, usually yellow and granulated, is linked by a thin tube to the pinkish white, lobed and coiled hermaphrodite duct, which in turn passes to the common duct. The seminal vesicle is partly lobed, uncoiled, pink to white and connected via a thin tube, alongside the albumen gland, to the common duct. The albumen gland is yellow to white, folded and lobed, closely attached to the seminal vesicle and hermaphrodite duct and surrounds the common duct with decreasing thickness to the accessory organ. The ovate, brown, patterned spermatheca (bursa copulatrix) is situated close to the epiphallus duct. The spermatheca tissue joining with the spermathecal duct can be expanded and stretched or collapsed and wrinkled. The sac tissue is thin, enclosing a granulated, brown gelatinous mass (no spermatophore present). The spermathecal and common ducts enter the genital atrium very close together and close to the genital pore. The common duct is ventral to the spermathecal duct. The junction of these ducts exists close to the accessory organ and is enclosed in anterior adductor muscle tissue. On the basis of the closeness of the duct joint, smallness of the genital atrium and greatly swollen epiphallus duct, Hubendick (1946) assigned *S. funiculata* to the "section Pachysiophonaria".

The spermatophore body is bulbous with a smooth, chitinous, transparent to translucent test. The head is bluntly pointed with a slight twist anteriorly. The pointed tail is shorter than half the spermatophore length (fig. 3e). Previous outlines of the reproductive system (Hubendick, 1945, 1946, 1954) and spermatophore (Hubendick, 1954) although incomplete (e.g. seminal vesicle and albumen gland not indicated), agree with the above descriptions.

Radula (pl. 3a-h)

The radula has a central tooth with an individually variable number of inner, mid and outer lateral teeth in longitudinal rows. The mean dentition formula is 43.1.43 (n = 17, sd = 7.9) with around 120 transverse rows (sd = 14.9). These rows are parallel and slightly curved (anteriorly convex; pl. 3c, g).

Hubendick (1954) provides the only comparative formulae indicating *S. funiculata* has about 44.1.44 teeth. Hubendick's values, based upon a small sample size, are explained as variations well within presented limits.

Of the 43 half row laterals, 7 (sd = 4.2) are inner, 17 (sd = 7.6) mid and 18 (sd = 3.1) outer lateral teeth means respectively. The total number of lateral teeth is related to the length of the shell (max. 54.1.54, shell length 22.0mm; -43.1.43, shell length 18.1mm; min. 34.1.34, shell length 15.1mm). However, the numbers of inner, mid and outer lateral teeth vary independently of animal dimensions and distributions. All teeth are bluntly concave posteriorly. The central tooth is narrow and weakly bicuspidate (often pointed) with a lower profile than the flanking laterals (pl. 3a). The base is broad with an anterior cleft and a posterior notched point providing interlocking articulation with adjacent central teeth. Mid and inner lateral teeth interlock with posteriorly and anteriorly aligned laterals. Outer laterals do not interlock between transverse rows. The space between rows increases to the ribbon edges associated with a gradual decrease in tooth size (pl. 3c, g). The space varies between individuals (pl. 3d, h) and posterior and anterior areas of the ribbon. Plate 3g shows the varying spacing of transverse rows close to the ribbon edge. All lateral teeth are broad based and bicuspidate on the mesocone with a longer inner cusp. Outer lateral mesocones are often multicuspitate. Increasing side denticle numbers, less elongated shape and increasingly stunted mesocones are transverse row features less accentuated from the central to the outer lateral teeth. Inner lateral teeth are elongated without flanking ento or ectocones (inner and outer side denticles respectively). The more

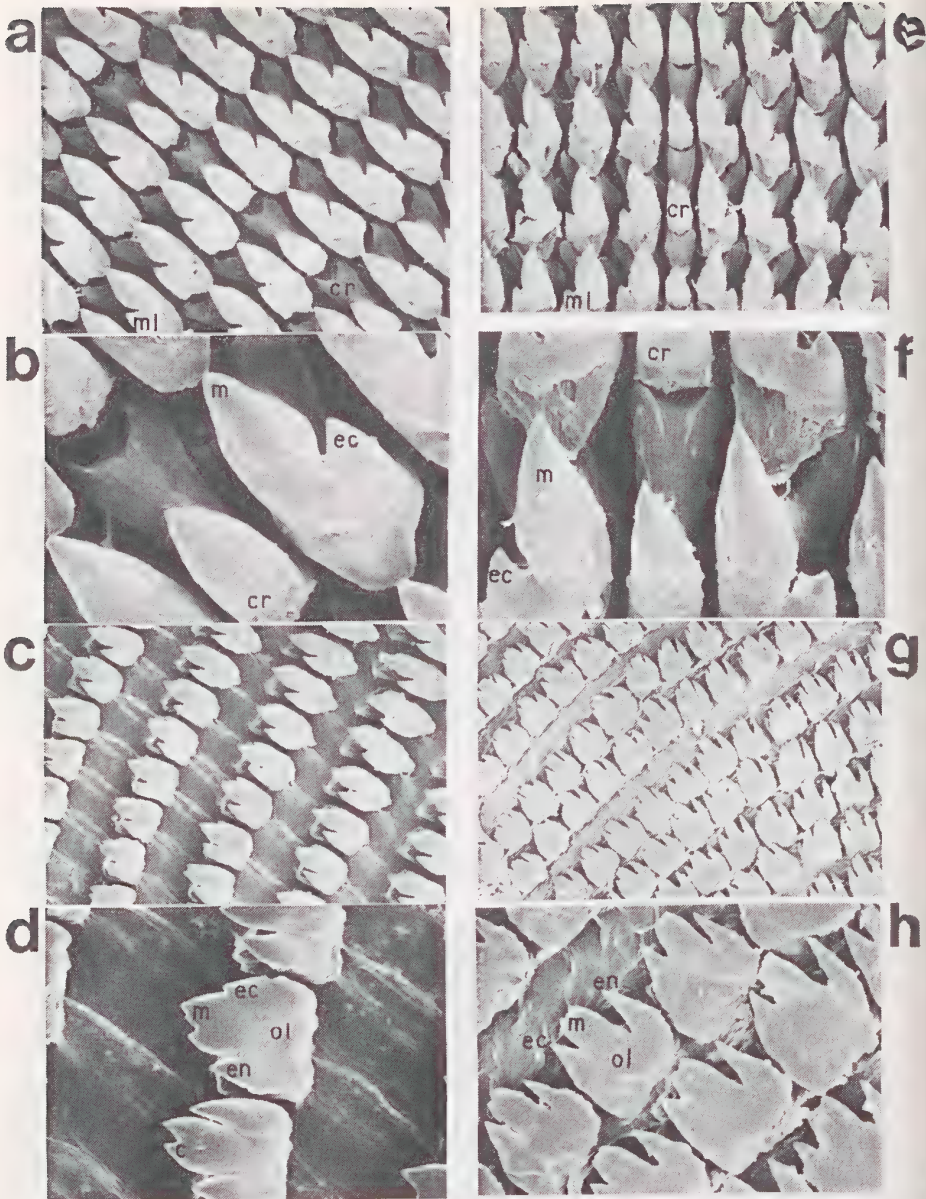


Plate 3.

Scanning electron micrographs of *S. funiculata* radulae:

Typical *S. funiculata* form, Red Bluff, near Lake Tyers, Vic., A.M. SEM stub 1005; a (x 500), b (x 1500) central and mid lateral teeth; c (x 500) outer and mid lateral teeth; d (x 1500) outer lateral teeth.

Nominal species *S. virgulata*, Tathra Point, Tathra, NSW., A.M. SEM stub 1004; e (x 500), f (x 1500) central and mid lateral teeth; g (x 500), h (x 1500) outer lateral teeth.

c — cusp, cr — central tooth, ec — ectocone, en — entocone, m — mesocone, ml — mid lateral tooth, ol — outer lateral tooth.

numerous outer lateral teeth have both an ecto and entocone while the mid laterals possess only an ectocone. The angle of separation from the mesocone of these side denticles is widely variable. Both side cones curve either towards or away from the mesocone (pl. 3g, h). The length and width of the separation cleft is also widely variable, both generally increase towards the ribbon edge (pl. 3c, d mid half ribbon area, pl. 3g, h ribbon edge). Aberrant outer lateral teeth are often present on both sides of the ribbon appearing as fused teeth with double mesocones. Not all individuals have the inner lateral teeth, most have increased numbers of mid laterals. The number is independent of the number of lateral teeth, for example, of two radulae with 54 half row laterals, one had no inner laterals while the other had 18. The same variability was noted for radulae with fewer numbers of lateral teeth. Inner laterals do not possess ento or ectocones.

Wet material (i.e. preserved in formalin) examined.

NSW.; Kilcare Beach, near Bouddi State Park (2); Syd.; Shelly Beach, near Manly (1); N. point of Tamarama Beach (8); Jobbon Head, S. side of Port Hacking (15+) Warden Head, Ulladulla (4); Mullimburra Point, Eurobodalla Shire (2); Tathra Point, Tathra (3); Vic.; Red Bluff, near Lake Tyers (4); Tas; Tasman Arch, S. end Eaglehawk Neck (4); total (43).

Dry material examined.

Qld.; Burnett Heads (6); Point Lookout, Stradbroke Is., Moreton Bay (7); NSW.; Ballina (1); Woody Head, Iluka (4); Clarence River (8); Minnie Water, S. of Clarence River (1); Yamba (1); Woolli (1); Woolgoolga (9); Port Macquarie (9); Hallidays Point, N. of Forster (4); The Caves Beach, S. of Swansea (3); Toowoomb, near The Entrance (15+); Catherine Hill Bay (2); Austinmer (5); McMasters Beach, N. of Broken Bay (5); Syd.; Palm Beach (3); Long Reef (7); Collaroy (15+); Middle Harbour (3); Balmoral, Sydney Harbour (11); Bronte (15+); Little Coogee Bay, Clovelly (5); Long Bay (3); Sandon Point, S. of Syd. (1); Coledale (15+); Warri Beach, Gerringsong (2); Sussex Inlet reef (3); Lake Burrill (15+) Broulee, S. of Batemans Bay (2); Kioloa Beach (3); Twofold Bay (15+); N. of Little River, Nadgee Faunal Reserve (3); Vic.; Bastion Point, Mallacoota (6); between Lake Tyers and Red Bluff, E. of Lakes Entrance (1); Lakes Entrance causeway (15+); Lakes Entrance (2); Walkerville, Waratah Bay (15+); Cape Paterson, Wonthaggi (1); Western Port (4); Flinders, Western Port (3); Fossil Beach, near Mornington, Port Phillip (2); Lorne (7); Apollo Bay (15+); Tas.; Point Sorell (5); Coles Bay (1); Pirates Bay, Eaglehawk Neck (1); Port Arthur (8); beach, 7 km S. of Swansea (1); Frederick Henry Bay (3); off Nubeena, Wedge Bay (3); total (290).

Specific variation

The conchological and radula features used in the original descriptions to define species of Siphonariidae are not considered sufficient specific criteria due to their wide intraspecific variability (Hubendick, 1946, 1950, 1954; Marcus and Marcus, 1960). Internal anatomical differences particularly in reproductive systems are specifically important. Such differences exhibit little intraspecific variation (Hubendick, 1945) and especially in reproductive systems are a basic feature of the species concept. Within the Siphonariidae, features of their reproductive systems, supported by gross shell form, are the criteria used by Hubendick (1946) and McAlpine (1952) to adequately designate generic, subgeneric and specific classification levels.

Compared to other species of "Pachysiphonaria", the typical *S. funiculata* and nominal *S. virgulata* are anatomically the same. The reproductive systems of each (fig 3a, b) have the muscular and swollen epiphallus gland and duct opening separately into the genital atrium and no flagellum, as is characteristic of the subgenus *Liriola* and "Pachysiphonaria". Specifically the nominal and the typical forms have identical spermatophore, large bulbous spermathecae, narrow spermathecal ducts and large epiphallus ducts. *S. (Liriola) tasmanica* from southern Australia, has a comparatively small spermatheca and epiphallus duct and gland with a long slender spermathecal duct (fig 3f). The common and spermathecal ducts open adjacently into the genital atrium similar to the typical *S. funiculata* and the nominal *S. virgulata* forms. *S. (Liriola) lessoni* (Blainville, 1824), from South America, has its epiphallus duct opening externally of the spermathecal duct and genital pore, a short thin common duct and a small epiphallus duct and gland

(Hubendick, 1946). These are distinct specific differences. The position and shape of the mantle cavity and reproductive and digestive organs are identical in the nominal and typical forms and only slightly differing from their cosubgenera.

The radulae examined exhibit similar tooth positioning and size (pl. 3a-h) with overlapping ranges of variation in teeth numbers and shape. This radula variation appears to be characteristic of the Siphonariidae in general (Hubendick, 1946). The mean dentition formula for the nominal species *S. virgulata* is 42.1.42 ($n = 13$, $sd = 6.4$) with 120 transverse rows ($sd = 18.5$). Of the 42 half row laterals 8 ($sd = 4.7$) are inner, 15 ($sd = 7.2$) are mid and 19 ($sd = 2.6$) outer lateral mean teeth numbers respectively. For the typical *S. funiculata* form the dentition formula is 45.1.45 ($n = 4$, $sd = 8.7$) with 124 transverse rows ($sd = 14.9$). The 45 half row laterals comprise 7 ($sd = 4.0$) inner, 17 ($sd = 7.5$) mid and 18 ($sd = 3.9$) outer lateral mean teeth numbers respectively. Although sample sizes are unequal, the typical form of *S. funiculata* appears to have more teeth and a greater variation in lateral teeth numbers compared to the *virgulata* form. However, the variation between both forms is within the more significant intraspecific variation indicating specific similarity.

The typical *S. funiculata* and nominal *S. virgulata* forms have the same dispersal, colouration and densities of white mucous and pigment cells. Their cephalic folds and pneumosomal lobes are similar in shape, thickness and positioning. Their mantles appear to be identical. These characteristics apart from colour, are considered generic rather than specific features.

Ecologically both forms occur at the same intertidal level and have merging geographical distributions (E. Vic.). The length of the breeding seasons of the typical *S. funiculata* and the nominal *S. virgulata* forms are unknown, although Creese (1980) suggests 5-6 months (about November to April) for the latter. This nominal species spawns by presumably ejecting from its large muscular epiphallus duct a pelagic egg mass (Creese, 1980) from which planktotrophic? veliger larvae develop after 6 days (Creese, 1980). This strategy may lead to greater dispersal. Cogenera *S. denticulata* and *S. baconi* Reeve, 1856 both lay flat spiral benthic egg masses. Although the egg mass of the typical *S. funiculata* form is undescribed, the fact that it hasn't been found on the shore (Creese, pers. comm.) and that the animal has an identical reproductive system to the *virgulata* form (fig. 3a, b), indicates it is probably also pelagic. It is reasonable to assume that both forms are not reproductively isolated, although little is known of the typical *S. funiculata* form's breeding cycle.

From tests of single dimension mean values the shell of the typical *S. funiculata* form is significantly longer, higher ($p < 0.01$) and wider ($p < 0.05$) with fewer but wider shell ribs ($p < 0.01$) than the nominal *S. virgulata* form (table 1). The variability within the mean values is similar for both forms. Large significant differences ($p < 0.001$) occur between each shell form for the quotient ratio values (table 1). These results indicate the shell of the typical *S. funiculata* form is generally bigger, particularly in height and length, and more variable in form. Both typical and nominal forms are however, not readily identified through each of these variables. Rib width and number, shell height and shell length are the most useful (pls. 1, 2). Such variation between the shells of anatomically identical animals may be either a clinal, subspecific or population variation relationship.

GEOGRAPHICAL VARIATION

From the preserved material examined, the external animal features, reproductive system and radula dentition exhibited no geographical variation. Variations in shell characteristics and dimensions (table 2) were considered the best indicators after Hubendick (1950) and Marcus and Marcus (1960).

For all the shell variables, except shell length:width ratio, rank analysis of geographical shell variance indicate significant differences (table 3) exist between the 6 regions tested (fig. 1). Differences between the shell length:width ratio for each region are considered homogenic ($H_s = 20.57$, $\chi^2 0.05 (14) = 25.00$, $p 0.05$). Other shell variables tested display heterogenic population sample variation with the greatest geographical variation present in shell height and width:height and length:width:height ratios ($p < 0.001$). The variation in each shell variable is clinal with a continuous, unidirectional gradient with

both homogenic and heterogenic differences between population samples. The number of ribs and the length:height ratio decreased in magnitude from Qld. to Tas. with a heterogenic change between Syd. and E. Vic. and around W. Vic. populations. The shell length, width, height and rib width all increase towards Qld. with heterogenic changes between N. NSW. and Syd. and in various positions between E. Vic. and Tas. samples. The width:height ratio decreases from either geographical extremity to a homogenic transitional Vic. shell form. Table 3 shows the overall change in shape and symmetry between the taller, less ribbed, longer and wider southerly distributed typical *S. funiculata* form and the northerly distributed nominal *S. virgulata* form. The transitional shell form can possess narrow ribs and a low shell height characteristic of the *virgulata* form with the narrow, high contrast brown and white external ribbing and lip colouration characteristic of the typical *S. funiculata* form (pl. 2d, e, f). Other transitional specimens can have low contrast light brown ribs and interstices (similar to pl. 2g, h).

The widest shell variability appears at the extremities of the geographical distribution (i.e. N.NSW. and Tas.) with inconsistent and nonaligned geographical population changes between shell variables. Overall such geographical variations indicate a clinal rather than a continuous conspecific population or an abrupt subspecific population change.

CONCLUSION

For these two forms to be considered subspecific, distributions would have to be allopatric (i.e. mutually exclusive but adjacent). If they are reproductively isolated (i.e. different breeding strategies and periods and intertidal levels) and with significant anatomical differences then the nominal species *S. virgulata* and the typical *S. funiculata* form would be valid species. As both forms are anatomically the same, not considered reproductively isolated and with wide shell variations and distributions merging from either geographical extremity of a cline, it is concluded they are sympatrically conspecific. *S. funiculata* has priority over the nominal species *S. virgulata*. The following nomenclature change is proposed.

Siphonaria funiculata Reeve, 1856
 = *blainvillei* Hanley, 1858
 = *virgulata* Hedley, 1915

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Table 1. Analysis of shell variation in *S. funiculata*.

Shell variable	typical form <i>S. funiculata</i>		nominal species <i>S. virgulata</i>		$F_{0.01(1,58)}$	F_5 significance
single classification, two tailed anova.						
(n = 30)	\bar{x}	sd	\bar{x}	sd	4	
Number of ribs	52.0	9.4	73.0	11.6	8.51	31.2 P<0.01
rib width mm	0.98	0.39	0.66	0.21	8.51	17.2 P<0.01
length mm	23.30	4.45	18.81	4.43	8.51	14.9 P<0.01
width mm	17.72	3.28	15.19	3.93	5.31 _{0.05(1,58)}	7.1 P<0.05
height mm	10.59	2.53	6.91	2.39	8.51	24.5 P<0.01
Wilcoxon two tailed, rank sum test. (non parametric)						
					$t_{29(0.001)}$	t_s
(n = 30)						
length : width	1.42	0.14	1.24	0.05	3.65	3.74 P<0.001
length : height	2.24	0.21	2.69	0.35	3.65	4.99 P<0.001
width : height	1.7	0.17	2.16	0.31	3.65	5.78 P<0.001
length : width : height	1.33	0.36	1.97	0.86	3.65	3.71 P<0.001

Table 2. Means and standard deviations of shell variables for geographical population samples.

shell variables	N. NSW.		Syd. NSW		E. Vic.		Westernport Vic.		W. Vic.		Tas.		n
	\bar{x}	sd	\bar{x}	sd	\bar{x}	sd	\bar{x}	sd	\bar{x}	sd	\bar{x}	sd	
rib numbers	72.6	9.5	69.4	9.3	60.0	6.8	53.9	18.2	48.0	9.92	51.67	11.1	15
ribwidth mm	0.47	0.09	0.68	0.21	0.73	0.19	0.84	0.28	1.15	0.30	0.95	0.39	10
length mm	14.6	3.7	18.7	3.0	17.4	2.2	19.9	4.0	20.0	2.7	35.5	3.9	15
width mm	11.6	3.0	15.4	2.4	14.3	2.0	15.9	3.8	15.1	2.1	18.2	2.9	15
height mm	5.7	1.8	6.8	1.6	7.6	2.1	9.3	2.8	8.7	1.5	11.3	3.2	15
length : width	1.26	0.14	1.22	0.1	1.22	0.12	1.27	0.1	1.33	0.06	1.29	0.06	15
length : height	2.56	0.34	2.82	0.25	2.47	0.68	2.19	0.26	2.32	0.12	2.08	0.18	15
width : height	2.04	0.28	2.31	0.28	2.04	0.61	1.73	0.23	1.75	0.14	1.61	0.15	15
length : width : height	0.25	0.08	0.19	0.03	0.17	0.05	0.15	0.05	0.16	0.02	0.12	0.02	15

Table 3. Kruskal-Wallis rank analysis of variance and order relationships for geographical populations.

shell variable	$H_s(\text{tie adj.}) \chi^2$	df	significance	multiple comparison test
number of ribs	34.90	30.58	0.01 > P > 0.001	1 = 2 > 3 = 4 > 5 = 6
rib width	25.69	21.67 (9)	0.01 > P > 0.001	1 < 2 = 3 < 4 = 5 = 6
length	34.00	29.14	0.01 > P > 0.001	1 < 2 = 3 = 4 < 5 < 6
width	27.76	29.14	0.05 > P > 0.01	1 < 2 = 3 = 4 < 5 < 6
height	43.51	29.14	P < 0.001	1 < 2 = 3 = 4 = 5 < 6
length : height	32.68	29.14	0.01 > P > 0.001	1 = 2 > 3 = 4 = 5 > 6
length : width	20.57	29.14	not significant	
width : height	40.54	29.14	P < 0.001	1 = 2 > 3 = 4 = 5 < 6
length : width : height	38.80	29.14	P < 0.001	1 = 2 > 3 > 4 = 5 = 6

for the multiple comparison between regions the signs < and > indicate heterogeneous partitions and magnitudes with = indicating homogeneous groupings.